



## In search of relationships between the acute adrenocortical response and fitness

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### ARTICLE INFO

#### Article history:

Received 5 March 2008

Revised 22 May 2008

Accepted 23 May 2008

Available online 2 June 2008

#### Keywords:

Glucocorticoids

Corticosterone

Cortisol

Stress

Environment

Performance

Fitness

Reproduction

Survival

### ABSTRACT

The assumption that the acute response to stress is adaptive is pervasive in the literature, but there is little direct evidence regarding potential positive fitness consequences of an acute stress response. If acute glucocorticoid (GC) elevation increases lifetime reproductive success (fitness), in what contexts does this occur, and through what combination of effects on annual reproductive output and interannual survival? Here we examine the framework under which most comparative acute GC studies fall, evaluate the commonalities of those studies in the light of expected fitness effects, and suggest methods to better examine the potentially beneficial effects of the acute GC response for free living animals. An overwhelming majority of papers from this area examine environmental–physiological–social effects on GC reactivity. Fewer evaluate intermediate performance measures (fitness proxies). We could only find 11 that directly examine GC effects on reproductive output and survival. The environment–GC–performance papers suggest that greater GC reactivity favors self-maintenance behavior (survival) at the expense of current reproduction. However, the two studies that directly address GC reactivity and fitness (2 of the 11) find the opposite effect (greater GC reactivity predicts lower annual survival). We suggest that it is time to move past simple evaluation of factors regulating GC secretion. These studies will be much richer and informative if researchers include performance and fitness measures. We especially support incorporating and testing ideas of context dependency, coping strategies, and possible fluctuating selection pressures when considering the fitness benefits of the acute GC response.

Published by Elsevier Inc.

### 1. Introduction

What constitutes a ‘good’ stress response?

More specifically, what aspects of the acute glucocorticoid (GC) response to any physical, physiological, or psychological challenge are beneficial for an organism? Current opinion posits that a combination of low baseline, fast increase, and rapid induction of negative feedback represents a ‘good’ response. This is good in an immediate, mechanistic sense. If GC elevation can be rapid and robust, and then cleared quickly, then GC-induced organismal output can occur quickly, while negative effects of sustained GC elevation do not occur. However, what constitutes a ‘good’ response in an evolutionary sense? That is, how do elevated GCs influence physiology and behavior to benefit reproduction or survival?

Ever since Selye formulated the “general adaptation syndrome” (Selye, 1937) it has been presumed that the early stages of the adrenocortical response to stress (resistance phase) should have adaptive value to free-living animals, even if the late stages (exhaustion phase) generally do not. Benefits of the early stages of the adrenocortical stress response—the acute GC response—are

presumed to facilitate escape from life-threatening situations such as attacks by predators, inclement weather, or social upheaval (Wingfield et al., 1998). The assumption that the acute response to stress is adaptive is pervasive in the literature, but there is little direct evidence regarding potential positive fitness consequences of an acute stress response.

It is assumed that *some* aspect of the acute GC response is beneficial, given its pervasive nature across vertebrates; in most vertebrates examined, GC levels increase between 4- and 10-fold within minutes in response to challenge. However, there is little evidence tying this increase to positive or negative effects on organisms’ fitness. If GC elevation increases lifetime reproductive success (fitness), under what contexts does this occur, and through what combination of effects on per-season reproductive output and interannual survival? Our understanding of the direct fitness effects of the acute GC response remains preliminary at best for at least two reasons. First, most work on stress biology has focused on the numerous deleterious consequences of *chronic* stress. There is little doubt that long-term activation of the hypothalamic–pituitary–adrenal (HPA) axis can damage health, reproductive function, and survival of captive and free-living animals (e.g., Boonstra and Singleton, 1993; Bradley et al., 1980; Creel, 2001; Lee and McDonald, 1985; Schoech et al., 1991; Smith and French, 1997). Such studies clearly reveal the potential costs of exposure to chronic

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stress. However, they do not provide direct empirical evidence either for fitness benefits of an acute stress response, or for mechanisms by which such benefits would be realized. Ultimately, such evidence needs to be sought in the field through studies specifically focused on the acute rather than on the chronic stress response. Second, the current generation of field studies typically stops short of directly linking inter-individual variation in acute GC physiology to differential fitness. Either they use fitness metrics that are only intermediate measures of performance (i.e., fitness proxies) but that are not themselves direct indices of fitness, or they demonstrate variation in GC physiology (e.g., among seasons, habitats, or taxa) and make logical arguments about how observed variants *should* be adaptive. Though informative, these approaches do not make the final connection to fitness. Consequently, relatively little is known about whether or how variation in acute GC physiology relates to variation in fitness, although the idea that an appropriately tuned acute adrenocortical stress response could lead to improved survival and/or reproductive success is widespread and intuitively appealing.

In this review, we consider measures of reproductive output (number of young born/hatched, fledged, reaching independence) and survival (annual or within season) to be ‘direct measures of fitness.’ It is seldom possible to obtain exact measures of individuals’ fitness; one can only achieve ‘fitness estimates.’ However, our effort here is to distinguish between intermediate performance measures (measures affected by GC secretion, but not directly associated with reproduction or survival) and more direct fitness estimates. Hence, we refer to measures of reproduction and survival as direct measures of fitness.

Our goal in this short forum piece is to examine the framework under which most comparative acute GC studies fall, to evaluate the commonalities of those studies in the light of fitness effects, and finally to suggest methods to better examine the potentially beneficial effects of the acute GC response for free living animals.

## 2. GC-fitness framework

The majority of comparative GC studies fall within three general categories, illustrated in Fig. 1 and described below:

1. **Regulation of secretion:** Environmental, developmental, physiological, and social effects that alter the acute GC response, discussing the expected fitness benefit of the change in response.

2. **Performance measures:** GC activation or suppression of intermediate performance measures, and the expected fitness benefit of the change in performance.

3. **Fitness effects:** Association of acute GC reactivity with direct measures of survival or reproductive output.

These three categories represent connections between the four aspects of the GC to fitness framework: environment – GC secretion – intermediate performance measures – fitness. Here is a theoretical example presenting all four aspects:

A theoretical example:

*Environment:* increased predator prevalence on territory.

*GC secretion:* variation in reactivity.

*Intermediate performance measure:* increased vigilance in more reactive individuals.

*Fitness measure:* greater survival probability in more reactive individuals.

In this example, studies may evaluate predator presence and GC reactivity, and then expect associations with increased vigilance and therefore greater survival probability. Alternatively, studies may directly measure vigilance behavior in addition to GC reactivity, but rarely will GC levels be taken all the way through the performance measures to a change in fitness parameters.

## 3. Literature review

Here we review studies falling into each of the three categories (Tables 1–3). Our purpose here is to look at the body of work as a whole, and evaluate what trends emerge in GC effects as related to secretion, performance measures, or fitness. This is not meant to be an exhaustive review of the literature, but a robust sampling of studies published over the last 15 years. The heavy bias toward bird studies simply attests to the extraordinary influence of John Wingfield’s conceptual and empirical contributions to the development of this field.

We identified relevant studies through three separate methods. First, we did cited reference searches from three classic papers regarding stress physiology across vertebrate classes (Ricklefs and Wikelski, 2002; Wingfield, 1994; Wingfield et al., 1998). Second, we performed several literature searches using different combinations of the terms: stress, glucocorticoids, corticosterone, cortisol, acute, response, performance, fitness, and survival. From those searches we identified studies appropriate for this review. And third, we searched reference lists from all of the above papers.

We were looking for studies that primarily focus on GC reactivity. However, there are some exceptions. In the performance and fitness sections, exogenous GC application was often not done in an ‘acute’ manner. Those studies are included here but should be interpreted with caution (see notes paragraph in Section 3.2). We

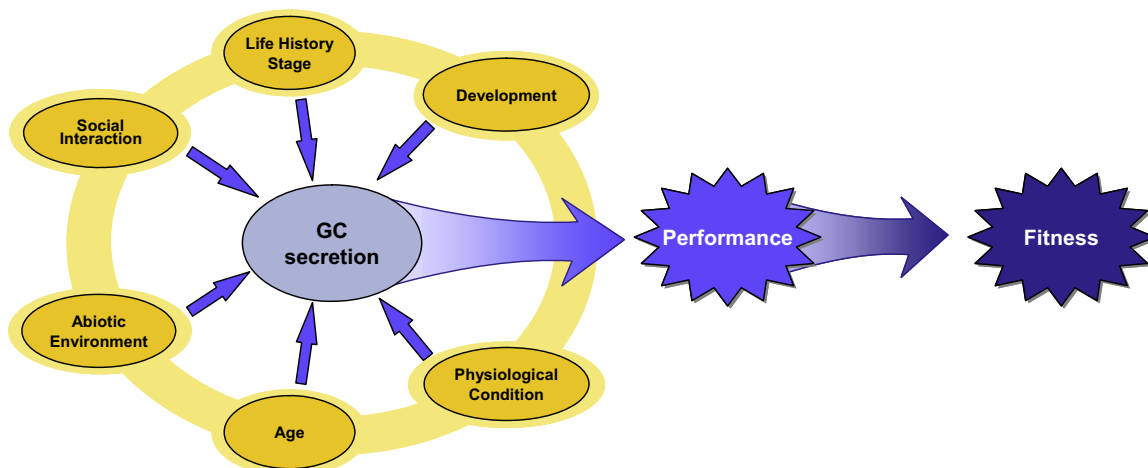


Fig. 1. A framework illustrating the relationships between environment, GC secretion, intermediate performance measures, and fitness.

**Table 1**  
Regulation of secretion

Animal model	GC-reactivity results	Expected fitness effect	Reference
<i>Reptiles</i>			
Green and Hawksbill turtles ( <i>Chelonia mydas</i> and <i>Eretmochelys imbricate</i> )	GC reactivity declines as female approaches lay	With greater investment in reproduction than males, females reduce GC reactivity to enhance reproductive success	Jessop (2001)
Green Turtle Juveniles and adults ( <i>C. mydas</i> )	GC reactivity greater in juveniles than adults	Favors survival in the more vulnerable age class	Jessop and Hamann (2005)
Galapagos Marine Iguana ( <i>Amblyrhynchus cristatus</i> )	Animals in poor body condition had elevated GC reactivity	Higher GCs may contribute to remodeling of body structure, i.e., reversed growth or bone resorption, contributing to increased survival	Romero and Wikelski (2001); Wikelski and Romero (2003)
Western Fence Lizard ( <i>Sceloporus occidentalis</i> )	Greater GC reactivity reflected poor physiological condition and extreme habitats, but GC reactivity is lower during breeding	During most of the year, poor internal or external conditions will lead to self-maintenance, but this response is suppressed to allow for reproduction	Dunlap and Wingfield (1995)
<i>Birds</i>			
Magellanic penguin ( <i>Spheniscus magellanicus</i> )	GC reactivity was negatively correlated with condition	When internal reserves decline, favor self-maintenance over breeding	Hood et al. (1998)
White Stork nestlings ( <i>Ciconia ciconia</i> )	GC reactivity increases with nestling age	GC elevation early in development may interfere with important developmental processes: decrease GC-increase survival	Blas et al. (2006)
American Kestrel females ( <i>Falco sparverius</i> )	Caloric restriction slows GC rate of increase and negative feedback	Poor condition birds have lower survival	Heath and Dufty (1998)
American Kestrel nestlings ( <i>F. sparverius</i> )	GC reactivity present by day 10 post-hatch, and increases with age	If food shortages common, mobilization of internal glucose stores will increase survival	Love et al. (2003a)
American Kestrel nestlings ( <i>F. sparverius</i> )	1 <sup>st</sup> hatched chicks show greater GC reactivity	1 <sup>st</sup> chick hatches a bit more developed, has greater GC reactivity, therefore, may beg more, get more food, grow faster, i.e., better survival	Love et al. (2003b)
Pectoral Sandpiper ( <i>Calidris melanotos</i> )	Within each species, the more parental sex had lower GC reactivity.	Increases reproductive success that season	O'Reilly and Wingfield (2001)
Semipalmated Sandpiper ( <i>C. pusilla</i> )			
Western Sandpiper ( <i>C. mauri</i> )			
Semipalmated Sandpiper ( <i>C. pusilla</i> )	Higher latitude populations had reduced GC reactivity	Favors reproduction over survival in limited and harsh breeding conditions	O'Reilly and Wingfield (2001)
Black- and Red-legged Kittiwake chicks ( <i>R. tridactyla</i> ; <i>R. brevirostris</i> )	Both nutritional and food restriction increase GC response	GCs elevate begging, increasing nutritional provisioning and therefore survival of chicks	Kitaysky et al. (2001a, 1999)
Common Tern ( <i>Sterna hirundo</i> )	GC reactivity declines with age	Lower residual reproductive value favors investment in current reproductive effort	Heidinger et al. (2006)
Dusky Flycatcher adults ( <i>Empidonax oberholseri</i> )	GC reactivity greater pre-nesting than post-nesting b. GC reactivity negatively correlated with body mass and fat class, positively correlated with winglength	Favors reproductive success during nestling phase, but correlation with parental care favors parental survival	Pereyra and Wingfield (2003)
Pied Flycatcher adults ( <i>F. hypoleuca</i> )	Higher latitude populations had reduced GC reactivity	Favors reproduction over survival in limited and harsh breeding conditions	Silverin (1998)
Pied Flycatcher females ( <i>F. hypoleuca</i> )	Females raising brood alone had greater GC reactivity	Likelihood of nest failure is high; female should favor self-maintenance	Silverin (1998)
Yellow Warbler ( <i>Dendroica petechia</i> )	Arctic males reduce GC reactivity during parental care, whereas temperate males do not	Lower GC reactivity favors the current breeding effort over survival	Wilson and Holberton (2004)
Willow Warbler ( <i>Phylloscopus trochilus</i> )	Higher latitude populations had reduced GC reactivity	Favors reproduction over survival in limited and harsh breeding conditions	Silverin (1997)
Hermit Thrush ( <i>Catharus guttatus</i> )	During migration, GC reactivity varies inversely with body condition	Lower energetic reserves will increase GC reactivity and promote feeding and fattening, i.e., promote survival during migration	Long and Holberton (2004)
White-crowned sparrow ( <i>Zonotrichia leucophrys</i> )	Greater GC reactivity associated with poor body condition	Self-maintenance behaviors will be activated more quickly when energetic reserves are low	Breuner and Hahn (2003)
White-crowned sparrow ( <i>Z. l. gambelii</i> )	Diel Cycle: GC reactivity greatest at the beginning of the day	Greater reactivity may correlate with greater behavioral response; options for responding to challenge are greater earlier in the day	Breuner et al. (1999)
White-crowned sparrow nestlings ( <i>Z. l. oriantha</i> )	GC reactivity increases with nestling age	GC elevation early in development may interfere with important developmental processes: decrease GC-increase survival	Wada et al. (2007)
Smith's Longspur males ( <i>Calcarius pictus</i> )	GC reactivity attenuated during parental/moult phase vs defense phase	Allows resources to be directed towards chicks (increased reproductive success) and feather growth (increased survival during migration)	Meddle et al. (2003)
Black-throated Sparrow ( <i>Amphispiza bilineata</i> )	The three species breeding in extreme desert environments had lower GC reactivity during the breeding season	Suppression of GC reactivity allows for reproductive success in spite of harsh environmental conditions	Wingfield et al. (1992)
Cactus Wren ( <i>Campylorhynchus brunneicapillus</i> )			
Curve-billed Thrasher ( <i>Toxostoma curvirostre</i> )			
<i>Mammals</i>			
Southern Elephant Seal pups ( <i>Mirounga leonine</i> )	GC reactivity increases with age	Low GC levels early in development protect developing organ systems, increase survival	Engelhard et al. (2002)
Vertebrates	Review of GC reactivity: amphibians and reptiles generally have greater GC reactivity during breeding; birds have lowest GC reactivity during molt; mammals have greater GC reactivity post-breeding	Energy Mobilization, Preparative, and Behavior Hypotheses; the data provide the best support for the Behavior Hypothesis (see review article)	Romero (2002)

**Table 2**  
Performance effects

Animal model	Performance effect of GCs <sup>a</sup>	Expected fitness effects	Reference
<i>Fishes</i>			
Rainbow Trout ( <i>Oncorhynchus mykiss</i> )	<b>1 h elevated GCs increases locomotor activity during territorial challenge</b> , while 48 h of elevated GCs decreases both activity and aggressive behavior during challenge	A rapid, active strategy may circumvent further stress (therefore increase survival), while prolonged stressors favor an energy-saving wait and see strategy (to increase survival)	Overli et al. (2002)
Atlantic Salmon offspring ( <i>Salmo salar</i> )	Maternal GC implant during egg development reduced embryo fork length, mass and yolk-sac volume	Smaller size indicates reduced survival probability	Eriksen et al. (2006)
<i>Amphibians</i>			
Northern leopard frog ( <i>Rana pipiens</i> )	50% increase in GC slowed growth and development	Sublethal disturbances can nonetheless incur significant detrimental effects (infer survival)	Glennemeier and Denver (2002)
<i>Reptiles</i>			
Galapagos Marine Iguana ( <i>A cristatus</i> )	Experimental GC elevation suppresses immune function	GCs redirect energy from immune to reproduction, increasing reproductive success	Berger et al. (2005)
Common Lizard juv ( <i>Lacerta vivipara</i> )	Maternal GC treatment decreased body size, condition, and growth in juveniles post-lay	Assume that maternal GC treatment decreases juvenile survival, but it increases it (see Table 3)	Meylan and Clobert (2005)
Common Lizard ( <i>L vivipara</i> )	GC implanted adults had higher energy expenditure, daily activity, and food intake	GC implants increased survival in males—see below (no explanation of ties to performance)	Cote et al. (2006)
Brown Anole males ( <i>Anolis sagrei</i> )	GC implant decreased territorial behavior, testis size, and spermatogenic activity	Increased GCs after social encounters may maintain subordinate social status (inc survival)	Tokarz (1987)
Side Blotched Lizard ( <i>Uta stansburiana</i> )	GC implant decreased aggressive behavior, independently of plasma testosterone	Turning off nonessential behaviors during challenge can increase survival	DeNardo and Licht (1993)
Side-blotched Lizard ( <i>U stansburiana</i> )	GC implant increased stamina, lowered resting metabolic rate, and shortened recovery time after exercise	Greater endurance and lower metabolic costs during stress incur survival advantage	Miles et al. (2007)
Red-sided Garter Snake ( <i>Thamnophis sirtalis parietalis</i> )	<b>Capture-induced GC increase does NOT alter reproductive behavior</b>	Decoupling GC levels from reproductive behavior will increase reproductive success during fasting	Moore et al. (2000)
<i>Birds</i>			
Japanese Quail ( <i>Coturnix coturnix japonica</i> )	Increased maternal GCs slows nestling growth and increases GC reactivity in those individuals as adults	Slower nestling growth lessens maternal burden and therefore increases maternal survival	Hayward and Wingfield (2004)
Black-legged Kittiwake chicks ( <i>R. tridactyla</i> )	GC implanted chicks increased begging rates, resulting in greater provisioning by adults	Greater provisioning results in higher probability of survival of chicks	Kitaysky et al. (2001b)
Black-legged Kittiwake adults ( <i>R. tridactyla</i> )	GC implanted adults spent more time away from the nest	Allocation of resources favor adult over chick, promoting adult survival	Kitaysky et al. (2001b)
Barn Swallows ( <i>Hirundo rustica</i> )	GC injection into egg reduced body size of nestlings	Smaller body size associated with lower likelihood of recruitment in the next year	Saino et al. (2005)
Pied Flycatcher ( <i>F. hypoeuca</i> )	GC implant decreased parental feeding rates, higher dose implants induced nest abandonment	Greater GCs result in lower reproductive success	Silverin (1986)
European Starling ( <i>Sturnus vulgaris</i> )	Increased Maternal GC increases male embryonic mortality, weight at hatch, and decreased cell-mediated immunity in males	The decline in numbers and quality of male offspring enhances maternal survival, and possibly survival of female young	Love et al. (2005)
Zebra Finch selected lines ( <i>Taeniopygia guttata</i> )	<b>Lines selected for greater GC reactivity have smaller adult body size</b>	Greater GC reactivity during development may incur costs in mate choice or male-male competition (i.e., lower reproductive success)	Roberts et al. (2007)
Song sparrow ( <i>Melospiza melodia</i> )	GC implants depressed territorial behavior and testosterone, but not luteinizing hormone	Challenging events may inhibit reproduction, but once the challenge is over, reproduction may continue without too much delay	Wingfield and Silverin (1986)
Tree sparrow ( <i>Spizella arborea</i> )	GC implants did not alter testosterone levels or territorial behaviors	Decoupling GCs from reproduction increases reproductive success in unpredictable environments	Astheimer et al. (2000)
White-crowned sparrow ( <i>Z. leucophrys</i> )	GC-implanted females produced more daughters	Daughters are more likely to reproduce regardless of quality.	Bonier et al. (2007b)
White-crowned sparrow ( <i>Z. l. oriantha</i> )	GC implant increases the time away from territory	Increased GC elevates threshold for acceptable environment for breeding, favors self-maintenance when conditions are poor	Breuner and Hahn (2003)
White-crowned sparrow captive ( <i>Z. l. gambelii</i> )	<b>Elevated GC levels in response to food removal associated with greater activity</b>	Greater circulating GC may increase foraging behavior to favor survival	Lynn et al. (2003)
White-crowned sparrow nestlings ( <i>Z. l. nutallii</i> )	<b>GC ingestion increases latency to beg within 20 min</b>	Greater GC reactivity may decrease survival	Wada and Breuner (in press)
White-crowned sparrow nestlings ( <i>Z. l. nutallii</i> )	48 h GC patch treatment slows growth	GCs incur fitness costs through smaller size or longer developmental time	Wada and Breuner (in press)
White-crowned sparrow ( <i>Z. l. gambelii</i> )	GC implants decrease activity with ad lib food, but increase activity under food restriction	When challenge includes low food ability, escape behavior may increase survival	Astheimer et al. (1992)
White-crowned sparrow ( <i>Z. l. gambelii</i> )	GC implants reduce nighttime metabolic rate	Under poor conditions lower metabolic rate at night will conserve energy, increase survival	Buttner et al. (1991)
White-crowned sparrow ( <i>Z. l. gambelii</i> )	Ingested GCs rapidly increase activity	Escape behavior during challenge may promote survival	Breuner et al. (1998)

(continued on next page)

Table 2 (continued)

Animal model	Performance effect of GCs <sup>a</sup>	Expected fitness effects	Reference
Smith's Longspur males ( <i>C. pictus</i> )	GC implant does NOT suppress territorial behavior	Decoupling GCs from reproductive behavior increases reproductive success in unpredictable environment	Meddle et al. (2003)
Mountain Chickadee ( <i>Parus gambelii</i> )	<b>GC ingestion increases seed retrieval rate</b>	GC surge may enhance memory retrieval and therefore survival	Saldanha et al. (2000)
<i>Mammals</i>			
Musk Shrew ( <i>Suncus marinus</i> )	Blocking GC secretion inhibits female reproductive behavior, behavior rescued with GC injection	GCs necessary to breed in an induced ovulator	Schimpl and Rissman (1999)

<sup>a</sup> It is likely that implants are representative of chronic stress. See 'notes' for performance effects. Bolded studies represent treatments more likely representing acute elevation of GCs.

Table 3

Direct fitness measures

Animal model	Fitness effect	Reference
<i>GC Reactivity and Survival</i>		
Galapagos Marine Iguana ( <i>A. cristatus</i> )	Greater GC reactivity (15 min) predicts annual survival: greater GCs = lower survival	Romero and Wikelski (2001)
European White Stork nestling ( <i>Ciconia ciconia</i> )	Greater GC reactivity in nestlings correlated with lower annual survival	Blas et al. (2007)
<i>GC Implant and survival or reproduction</i>		
Common Lizard ( <i>L. vivipara</i> )	Males with GC implants had higher annual survival in outdoor enclosures	Cote et al. (2006)
Pied Flycatcher ( <i>F. hypoeuca</i> )	GC implant into parents (post lay) decreased number of young fledged, higher dose implants induced nest abandonment	Silverin (1986)
<i>Endogenous CORT and Survival</i>		
Side-blotched lizard females ( <i>U. stansburiana</i> )	Higher GC levels correlated with greater survival to second clutch	Comendant et al. (2003)
Cliff Swallow ( <i>Petrochelidon pyrrhonota</i> )	Early and mid-breeding season GC levels negatively related to annual survival	Brown et al. (2005)
European rabbit ( <i>Oryctolagus cuniculus</i> )	GC levels after 2–4 weeks of captivity were positively correlated with survival in the wild over the next 30 days	Cabezas et al. (2007)
<i>CORT-induced 'Maternal Effects'</i>		
Atlantic Salmon offspring ( <i>S. salar</i> )	Maternal GC implant during egg development caused increased mortality in offspring	Eriksen et al. (2006)
Common Gecko ( <i>Hoplodactylus maculates</i> )	Maternal GC treatment changed offspring produced from 80% of embryos to 0% of embryos	Cree et al. (2003)
Common Lizard juveniles ( <i>L. vivipara</i> )	Maternal GC treatment increased juvenile male's survival to the next year (free-living after birth)	Meylan and Clobert (2005)
Barn Swallow ( <i>H. rustica</i> )	GC injection into egg reduced hatching success	Saino et al. (2005)

did not include studies that measured fecal or plasma baseline levels (except three references noted as such in Section 3.3). Both fecal and baseline studies offer results that are difficult to interpret in light of acute GC secretion. Unfortunately these limitations significantly reduced our mammalian examples. We did not incorporate biomedical studies, as we feel that would be most appropriately done in a separate review.

### 3.1. Regulation of secretion

The most common method used to evaluate the acute adrenocortical response to stress is collecting serial blood samples during a standardized protocol of handling and restraint. This method allows one to examine individual variation in the reactivity of the HPA axis to a standardized stressor. The resulting data allow for comparison of multiple aspects of the adrenocortical response to stress, including baseline glucocorticoids (GCs), maximum GC measured over the handling and restraint stress, rate of GC increase (see 'notes' below), and total amount of GCs secreted—an integration of GC levels over the entire period of sampling. Across the studies examined, maximum GC measured is the most commonly evaluated aspect of stress reactivity. It is important to note the one critical assumption of this sampling regime: that individual variation in GC response to capture and handling represents variation among individuals in responding to more natural challenges.

A summary of fitness expectations from these papers mirrors the expectation that glucocorticoids mediate the tradeoff between

reproduction and survival (Ricklefs and Wikelski, 2002). Environmental factors associated with increased GC reactivity are thought to promote survival (through self-maintenance behaviors) at cost to current reproduction. Alternatively, environmental factors associated with suppressed GC reactivity are thought to promote reproduction at cost to survival.

*Notes:* We would like to note that rate of GC increase is a difficult metric to evaluate precisely. Older papers tended to take plasma samples at 0, 5, and 10 min, giving a fairly robust measure of how quickly GC levels became elevated after initial disturbance. However, current studies usually only evaluate 0 and 30 min, or 0, 15, and 30 at best. This leads to a loss of information crucial to the calculation of rate of increase. When samples are taken only at 0 and 30, rate of increase is measured as the change in hormone level between baseline and 30 min divided by 30 min. Early studies demonstrate that species may reach near maximum levels by 10 min (Wingfield et al., 1994, 1992), and so dividing by 15 or 30 leads to inaccurate quantification of the rate of increase. We believe that a better use of these data is to report absolute differences or fold-increase (see Romero, 2004, for in depth discussion). This is similar to the maximum GC levels measured, but corrected for differences in baseline. This measurement has been used to compare across species (e.g., Wingfield et al., 1995), as baseline levels can vary across species, masking or extending perceived differences in stress-associated levels. If measurement of rate of increase is a specific goal of the study, we recommend obtaining blood samples appropriate to the period of initial glucocorticoid increase for that species (i.e., 5 and 10 min in passerines).

### 3.2. Performance effects

The performance effects of GCs will certainly be context dependent (see Orchinik, 1998, for a clear discussion of this issue). Hence, it is difficult to find generalizations from data collected across seasons, sexes, ages, phenologies, and vertebrate classes.

However, a few overarching themes emerge. Experimental GC increase can increase self-maintenance behavior, presumably increasing survival with cost to current reproduction (Astheimer et al., 1992; Breuner et al., 1998; Breuner and Hahn, 2003; DeNardo and Licht, 1993; Lanctot et al., 2003; Lynn et al., 2003; Tokarz, 1987). However, GC increase had no effect on breeding behavior in several species, presumably favoring the continuation of breeding in spite of challenging conditions (Astheimer et al., 2000; Meddle et al., 2003; Moore et al., 2000). Contrary to all previous findings, acute GC increase may be required or simply beneficial for breeding in three species (Berger et al., 2005; Orchinik et al., 1988; Schiml and Rissman, 1999), stimulating reproductive behaviors or redirection of resources away from energy-draining systems such as immune function. Finally, elevated GCs appear to favor maternal survival (matching chick need to maternal ability), while producing mostly detrimental effects in offspring (Bonier et al., 2007a; Eriksen et al., 2006; Hayward and Wingfield, 2004; Love et al., 2005; Meylan and Clobert, 2005; Roberts et al., 2007).

In spite of the variety of results, the common themes suggest a similar role for GCs as implied by the 'regulation of secretion' results. That is, they support a role for GCs as a mediator of the trade-off between reproduction and survival. Acute GC elevation appears to reduce reproductive behavior in favor of self-maintenance behaviors, promoting survival at the cost of current reproductive success.

*Notes:* Performance effects of GCs were compared between control and GC-treated animals. Exogenous GC treatment should be one of the best ways to test relationships between acute stress reactivity and performance measures. However, one runs into trouble when deciding which method of GC treatment to use. Silastic implants filled with GCs are the most common method; however, this method elevates GCs with a constancy and duration more representative of a chronic stressor than an acute GC response. So it remains a question: do GC implants distinguish performance effects relative to acute stress reactivity, or are they only representative of GC effects within a chronic framework?

A few studies evaluated rapid, transient changes in GC level, more easily comparable to acute GC reactivity. Consumption of a GC-injected meal worm or grub can increase activity, seed retrieval, and latency to beg (Breuner et al., 1998; Saldanha et al., 2000; Wada and Breuner, 2008). Application of a GC-soaked patch to bare skin increases activity, slows growth and reduces testosterone, (Belliere et al., 2004; Knapp and Moore, 1997; Wada and Breuner, 2008). One study tested multiple methods of GC treatment, and found that while 1 h of GC treatment increased activity, 48 h had the opposite effect (Overli et al., 2002, in rainbow trout); the authors argue that the appropriate response to immediate challenge varies significantly from the appropriate response to a prolonged challenge.

To determine which method of GC application best represents acute stress reactivity, the field would have to agree on definitions of acute and chronic responses. Those working most closely with environment-GC-performance studies have a difficult time agreeing: if the onset of a challenge is slow (such as a storm, where snow cover brings food availability down to zero over hours, not minutes), is a slower increase in GCs representative of an acute response? Is chronic stress solely defined by when the challenge lasts long enough to override negative feedback? If a chronically stressed animal (through social subordination or chronic food shortage) shows further response to a different stressor (i.e., Dall-

man et al., 1994; Romero and Wikelski, 2001), do we evaluate the increase in the same manner? The biomedical/mammalian field has various answers to these questions, however their conclusions are rarely translated into free-living vertebrates. Hence, this is an area needing further discussion in the comparative field.

### 3.3. Direct fitness measures

Results from secretion and performance studies primarily support a role for acute GCs in promoting survival over reproduction. Do direct fitness measures reflect this role? We found 11 studies that compared endogenous or manipulated GC levels to direct measures of fitness.

Only two of these 11 studies examined the relationship between GC reactivity and subsequent survival: both found that greater reactivity predicts lower annual survival. These data directly contradict the assumptions regarding GC reactivity and survival presented in Sections 3.1 and 3.2.

Circulating corticosterone levels (either endogenous or experimentally modified) show mixed results. In European rabbits, common and side-blotched lizards, greater circulating GCs correlated with greater survival (Cabezas et al., 2007; Comendant et al., 2003; Cote et al., 2006). However, in cliff swallows, higher circulating GC levels correlated with reduced survival (Brown et al., 2005).

Effects of maternal GCs on offspring appear to be time-frame dependent. Maternal or egg GC treatment decreased offspring survival when measured at the embryonic or post-natal level (Cree et al., 2003; Eriksen et al., 2006; Saino et al., 2005), while similar treatment increased survival from independence to the next breeding season (Meylan and Clobert, 2005). These data support the maternal/offspring match hypothesis; this hypothesis posits that maternal glucocorticoids may reduce offspring growth and male survival in stressful conditions; however this reduction may better match maternal ability to provide resources in stressful environments, increasing the likelihood of offspring survival over the long term (Breuner, in press; Love and Williams, in press).

*Final Note:* In all three sections, we consider only total hormone levels. Recent work has suggested the alteration in both plasma binding globulin levels and intracellular GC receptors may also regulate the resulting response to GC elevation (Breuner et al., 2006, 2003; Breuner and Orchinik, 2001, 2002; Love et al., 2004). It will be interesting to see if inclusion of these factors in our overall analysis of stress reactivity will help clarify the links between environment, GC response, performance and fitness. This approach could also provide a consequence-based (i.e., via both performance and fitness) way of evaluating what role binding globulins play in the function of GCs, complementing direct molecular, cellular, and physiological studies of this issue.

## 4. Summary of studies

Over the last two decades, hormonal and performance data have suggested that glucocorticoids help regulate the trade-off between survival and reproduction. These studies led to the logical (but largely untested) conclusion that acute glucocorticoid secretion favors self-maintenance behavior at the expense of current reproduction. If an organism must reproduce in unpredictably severe environments, then GC reactivity must be reduced, or decoupled from reproductive behavior. There are extraordinarily few studies that directly test these relationships: of the two that examine GC reactivity and survival, both contradict the general paradigm (increased reactivity predicts lower annual survival).

We would like to finish this section with some thoughts on context dependency. Clearly, the relationship between GCs and survival is context dependent. Cote et al. (2006) note that in marine iguanas, higher GCs predicted lower survival, while in common liz-

ards, higher GCs increased survival. However, in the common lizards, food was not limited. It is entirely possible (in fact likely) that environmental context will broadly influence GC effects on fitness. Blas et al. (2007) suggest that variability in GC reactivity may be maintained if 'high and low GC responders represent alternative coping strategies [e.g., risk averse vs. risk tolerant (author addition)], with differential adaptive value depending on environmental conditions.' In severe weather years, greater GC reactivity may be favored as conditions deteriorate quickly. However, in benign years, greater GC reactivity may lead to premature abandonment of young, when survival is not at risk. Interannual variation in weather could thus lead to fluctuating selection on GC reactivity and help maintain variation of this trait. Further, residual reproductive value may determine whether animals are risk averse vs. risk prone in their GC reactivity. The ideas of context dependency, coping strategies, and fluctuating selection pressures need to be kept in the forefront of analyses of these data.

## 5. Conclusions and suggestions

It is time to move past simple evaluation of factors regulating GC secretion. Studies of GC reactivity will be much richer and informative if one includes performance and fitness measures.

In particular, it is necessary to extend field studies to include direct evaluations of relationships between inter-individual variation in acute stress physiology and fitness (reproductive success and survival). Developing a sequence of connections, integrating stress physiology with intermediate performance measures, and integrating these measures with direct measures of fitness, can reveal how GC system function affects fitness as well as the performance-related mechanisms by which these effects are mediated. We also suggest incorporating measures of repeatability and heritability of GC reactivity into current studies (i.e., Cockrem and Silverin, 2002; Roberts et al., 2007; Satterlee and Johnson, 1988); inclusion of these measures will strengthen the evidence for selection acting on these GC traits.

We believe several benefits can accrue from the approach we suggest. First, it should become possible to evaluate the long-standing presumption that variation in features of the acute adrenocortical stress response relate to fitness, as well as to identify what aspects of performance are most likely to be responsible for any fitness consequences that do emerge. Second, it should be possible to determine whether selection is operating on features of stress physiology in populations, and to identify the nature of that selection (e.g., directional, stabilizing, fluctuating). And lastly, it should be possible to be far more objective about what constitutes "good" and "bad" stress response features under particular environmental circumstances, because fitness will be used as the final arbiter rather than our intuitive assessment of what should be good or bad. In this regard, it is particularly important to consider life history, because the acute and chronic stress responses may not constitute a simple good/bad dichotomy. For instance, under some circumstances, such as for semelparous animals, the chronic response may have positive fitness consequences despite accelerating debilitation and death. It will be particularly interesting to consider variation in GC reactivity in light of new conceptual frameworks such as life history state diversity (Wingfield, 2008) since transitions among life history states are key aspects of performance that will affect fitness in different ways. For instance, the transition from the breeding life history state to plumage molt represents a switch from investment in current reproductive effort to investment in an adult survival—precisely the type of trade-off that variation in GC responsiveness is expected to affect.

Taken together, we believe that these approaches constitute some of the most important and logical next steps for research

on acute adrenocortical stress physiology. Progress in this area will not only fill in long-standing gaps regarding the adaptive significance of the acute adrenocortical stress response, but will also help to direct future studies and provide predictive power as to potential responses of animal populations to new environmental challenges.

## Acknowledgments

We would like to thank R. Sprague, J. Sprague, C. Williams and M. Bowlin and two anonymous reviewers for editorial comments. The work leading to the development of this review was supported by NSF IBN 0236536 and 0235911 to C.W. Breuner and T.P. Hahn, respectively.

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